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ANALYSIS OF THE COMMON THRESHER SHARK, Alopias vulpinus, IN THE CALIFORNIA BIGHT

by

Doyle Alan Hanan

ADMINISTRATIVE REPORT LJ-84-10C

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Analysis of the Common Thresher Shark, *Alopias vulpinus*, in the California Bight

Doyle Alan Hanan

California Department of Fish and Game
c/o Southwest Fisheries Center
La Jolla, California 92038

April 1984

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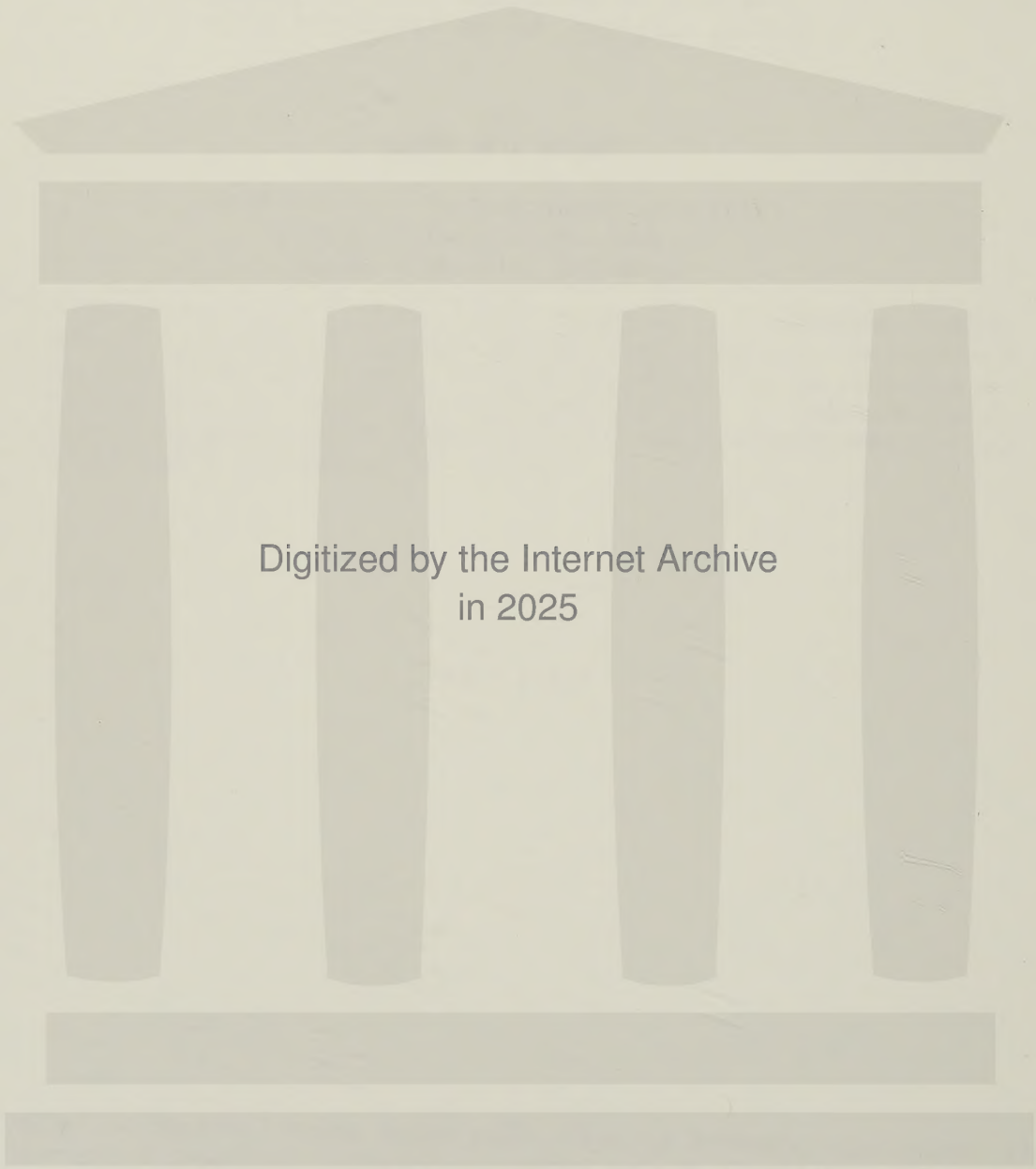

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La Jolla, California 92038

INTRODUCTION

Since about 1977, a new fishery using large mesh gill nets of nearly a mile in length has developed off the coast of California. The fishery targets on pelagic sharks (common thresher, Alopias vulpinus, and bonito, Isurus oxyrinchus). However, the expansion of this fishery from the initial ten or fifteen participants to the current 200+ can probably be attributed to the catches of swordfish, Xiphias gladius, taken incidentally with the sharks. The rapid growth in the shark fishery concerned many sport and commercial fishers, as well as fishery biologists. Concern ranged from allocation of catches and conflict with existing fisheries to the possibility of overfishing and loss of the exploited stocks.

In an attempt to answer these concerns, the California state legislature passed Assembly Bill 2564 (Kapiloff), which directed the Department of Fish and Game (DFG) to study the drift gill net fishery and provided funding for the program via permit fees for the drift gill net shark fishery and the harpoon swordfish fishery, along with an additional privilege tax on thresher and bonito shark landings. The legislation also required all drift gill-net shark permittees to submit daily logs of their fishing activities. As required by the legislation, the DFG established the Pelagic Shark-Billfish Monitoring Project to place observers on board the fishing vessels to gather data on the catch and the fishing operations. Length frequency data were taken at the docks and fish markets as the catches from drift gill net vessels were unloaded. Project findings were summarized in a manuscript presented to the California legislature in 1982.

Another DFG marine biologist, under contract to National Marine Fisheries Service, was assigned to describe the condition of the thresher shark resource and the risk due to harvest. This project analyzed the available data using modelling techniques. The results of that study along with summaries of the available data are presented in this final report. The model developed during the study is presented as a scientific manuscript (Appendix A), which has been prepared and submitted for publication in a scientific journal.

At the beginning of these studies, very little information existed about the thresher shark. Aside from the two DFG studies, only one other research project was in process; Professor Gregor Cailliet of Moss Landing Marine Lab was conducting an ageing study for commonly taken sharks off California. The study was based on vertebrae and shark length information from fresh dockside samples and preserved museum samples. A summary of his results (Cailliet and

Bedford 1983) are presented herein as a graph of the von Bertalanffy growth equation (Figure 1).

The sources of data for this final report are:

1. Data collected by the DFG observer program including biological data collected at sea and at the docks or fish markets (1981-1982),

2. Skipper's daily logs (1981-1982), and

3. DFG landing receipts (pink tickets 1977-1982).

THE FISHERY

Thresher sharks are fished off the coast of California from the border with Mexico to San Francisco by commercial gill net and infrequently by hook and line sportfishing enthusiasts. Thresher sharks are also caught incidentally in the eastern North Pacific by Japanese and Korean longline vessels, which target mainly on marlin, swordfish, and tunas. Consequently many of the thresher sharks landed off California have longline hooks imbedded in their mouths, indicating encounters with those other fisheries.

Since 1977, the catches of thresher sharks (Table 1) have increased annually, with a fairly distinct seasonal peak in the summer months (Figure 2). Since effort data are available only for 1981 and 1982, annual catch per unit effort (CPUE) analysis is not meaningful. However, monthly CPUE values indicate a peak in summer months (Table 2). Length frequency histograms (Figure 3) of the 1981 and 1982 landed catch samples show a slight shift to smaller thresher sharks in 1982. This shift is also seen in the average weight of landed thresher sharks, which was 132 pounds for 1981 and 99 pounds for 1982. With only two years of data, this shift cannot be interpreted as a trend; but these data do indicate a need to closely monitor the fishery, since shark fisheries can collapse rapidly (Ripley 1946; Holden 1974).

Thresher sharks are headed, tailed, eviscerated, and cleaned at sea by the gill net operator. The landing price ranges between 0.80 and 1.00 per pound, making the thresher shark component of the drift gill net fishery worth about two million dollars annually. Thresher shark steaks or filets retail between 3.25 and 4.25 per pound depending on season and quality of the product.

MANAGEMENT

The original California legislation (Assembly Bill 2564, Kapiloff) regulating the shark drift gill net fishery expired in September 1982. Thus, new legislation for this fishery was introduced and passed by the California legislature in 1982. This legislation (Senate Bill 1573, Beverly) establishes new regulations regarding the use of drift gill nets to take shark and swordfish. The legislation limits entry into the drift gill net shark and swordfish fishery to permittees under the 1980 legislation or those who had landed at least 5000 pounds of swordfish in each of the calendar years from

1977 to 1981. Ultimately, the legislation limits the number of permittees to 150, and once attrition has reduced the total number of permittees below 150, a drawing among qualified applicants will be held for the available permits. The legislation restricts drift gill net lengths to 6000 feet or less and after 1985, to a stretched mesh size greater than 14 inches. The legislation closes the fishery from February through April and closes specific ocean areas during other specified times of the year. It continues the additional privilege tax of 0.01 per pound on landings of thresher and bonito shark and continues the 150.00 permit fee for drift gill net shark and swordfish permits and for swordfish harpoon permits. The legislation also sets forth conditions under which the DFG must evaluate the resource to determine if a fishing or ocean area closure is necessary based on the state of the shark and/or swordfish resources.

BIOLOGICAL INFORMATION

Common thresher sharks occur throughout much of the Pacific Ocean, and probably concentrate in nearshore waters (Strasburg 1958). Because almost no tagging studies have been attempted on thresher sharks in the Pacific, the actual structure of the stock or stocks is unknown. This problem of stock structure is probably the most important unknown aspect of the biology of the thresher shark resource in the Pacific Ocean, since any assessment for management purposes must consider that element. Longline hooks in the mouths of thresher sharks caught off California, indicate that these fish have migrated from areas where longline fisheries exist, such as off Baja California. Essentially, these hooks could be considered tags implying a migratory pattern which extends at least from the Revilla Gigedo Islands, Mexico to Monterey, California and most likely includes many other areas of the Pacific Ocean.

Common thresher sharks appear to be long-lived and to have fairly low natural mortality rates. No determination of fishing mortality rates have been attempted, but the sustainable fishing mortality models developed during this study (Appendix A) suggest that those rates would have to be quite low to afford a sustaining population. Comparison of the von Bertalanffy growth curve (Figure 1) to the histograms of market samples (Figure 3) shows that the drift gill net fishery in the California Bight catches almost exclusively immature thresher sharks. The impact of fishing those age classes will depend on the thresher shark stock structure.

Thresher sharks are ovoviviparous and bear two to four live young. Females reach sexual maturity at seven to nine years, while males appear to mature somewhat earlier (Dennis Bedford, DFG, pers com). In uteri, pups usually have stomachs full of yolk, implying ovaphagism. The pups are born in the spring months after a nine month gestation period and at birth have already reached total body lengths of 1-1.5 meters.

RESULTS OF MODELING

The major accomplishment of this study was the development of a modeling method which allows the prediction of sustainable fishing mortality rates with minimal data about the stock in question (Appendix A). The model assumes that

a harvested stock will tend to offset harvest losses in one of several density-dependant strategies. These strategies might involve increased recruitment to the stock or increased survival rates in the animals already recruited; but ultimately the goal is to return the stock to an equilibrium situation, where recruitment balances stock losses to harvest and natural mortality. The sustainable harvest mortality is then equal to the density-dependant production, a quantity that can be described by an equation based on standard demographic techniques.

Because thresher sharks appear to have high survival rates combined with a low fecundity rate possibly controlled by ovaphagism; it was hypothesized that the only density-dependant response likely to offset a harvest of thresher sharks would be a decline in the age of maturity. This decline would have the effect of increasing the net fecundity of the reproducing stock. Using a range of feasible survival rates for a hypothetical stock of thresher sharks (Appendix A), the model shows that the stock could withstand a low fishing mortality. The key term in this finding is stock, which is not known for thresher sharks. Therefore, we can only speculate about the effect of the drift gill net fishery on the thresher shark population.

Baronov's catch equation (Ricker 1975, equation 1.17) is used with an estimate of the total area fished by the California drift gill net fleet (72,000 square nautical miles) to make a density prediction. First assume that the adult survival rate in these thresher sharks is 0.85 annually, that they mature about age eight, and that the age of maturity decreases by one year in response to the harvest. These population parameters, when substituted into the sustainable fishing mortality model, (Appendix A) project 0.013 for the sustainable fishing mortality rate. If we assume that the gill net fishery is fishing at this conservative rate, the total catch and the above described population parameters, when substituted into the catch equation, predict an average population size of 1.5 million thresher sharks required to maintain the gill net fishery at current catch rates (18,292 thresher sharks per year). Dividing this population estimate by the area fished implies a population density of 21 thresher sharks per square nautical mile within the fishing range.

If we assume that an equal number of thresher sharks are being caught off Mexico and include that area in the calculation, the density drops to 10 thresher sharks per square nautical mile. Both of these density estimates seem high; and yet, both densities are based on conservative estimates and assumptions. Clearly two scenarios are possible. Either there is a great deal of immigration from a large, perhaps Pacific-wide stock or the thresher sharks are being fished at a rate not sustainable by a local stock. The large immigration theory seems most logical, since many locally caught thresher sharks have longline hooks in their mouths and Alopias vulpinus is a Pacific-wide species.

As shown above, this report identifies the need for additional research into stock structure, migratory patterns, and biological data for vital rate determinations. With these additional data, the status of both the stock and the fishery can be analyzed with a higher degree of confidence.

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Table 1. Total thresher shark landings in pounds from DFG landing receipts.

YEAR	#RECEIPTS	POUNDS
1977	349	129522
1978	433	302054
1979	745	735536
1980	880	1407069
1981	1632	1973518
1982	1851	2192134

TABLE 2. Monthly catches and fleet days of drift gill net effort from summaries of skipper's logs and landing receipts.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	TOTAL
1980 Observer Data													
# Threshers										102	6	0	108
# Observer Days										38	22	4	64
1981 Observer Data													
# Threshers				115	40	413	7	8	3	30	0	2	618
# Observer Days				14	15	25	11	22	22	37	4	3	153
Logbook Data													
# Threshers				2247	4312	2926	943	751	1411	1502	333	295	14720
Lbs X 1000				286	513	287	156	134	154	284	65	44	1923
Days Fished				398	767	600	517	589	784	1213	407	223	5498
# Threshers/Day				5.7	5.6	4.9	1.8	1.3	1.8	1.2	0.8	1.3	2.7
1982 Observer Data													
# Threshers		13	0	147	19		5				0		184
# Observer Days		5	7	9	13		7				5		46
Logbook Data													
# Threshers	118	2377	531	1039	4878	6629	1000	1622	1979	973	398	319	21863
Lbs X 1000	12	258	145	104	261	737	177	234	252	72	24	1	2277
Days Fished	29	167	179	306	783	786	756	3087	1392	1929	1435	790	11639
# Threshers/Day	4.1	14.2	3.0	3.4	6.2	8.4	1.3	0.5	1.4	0.5	0.3	0.4	1.7

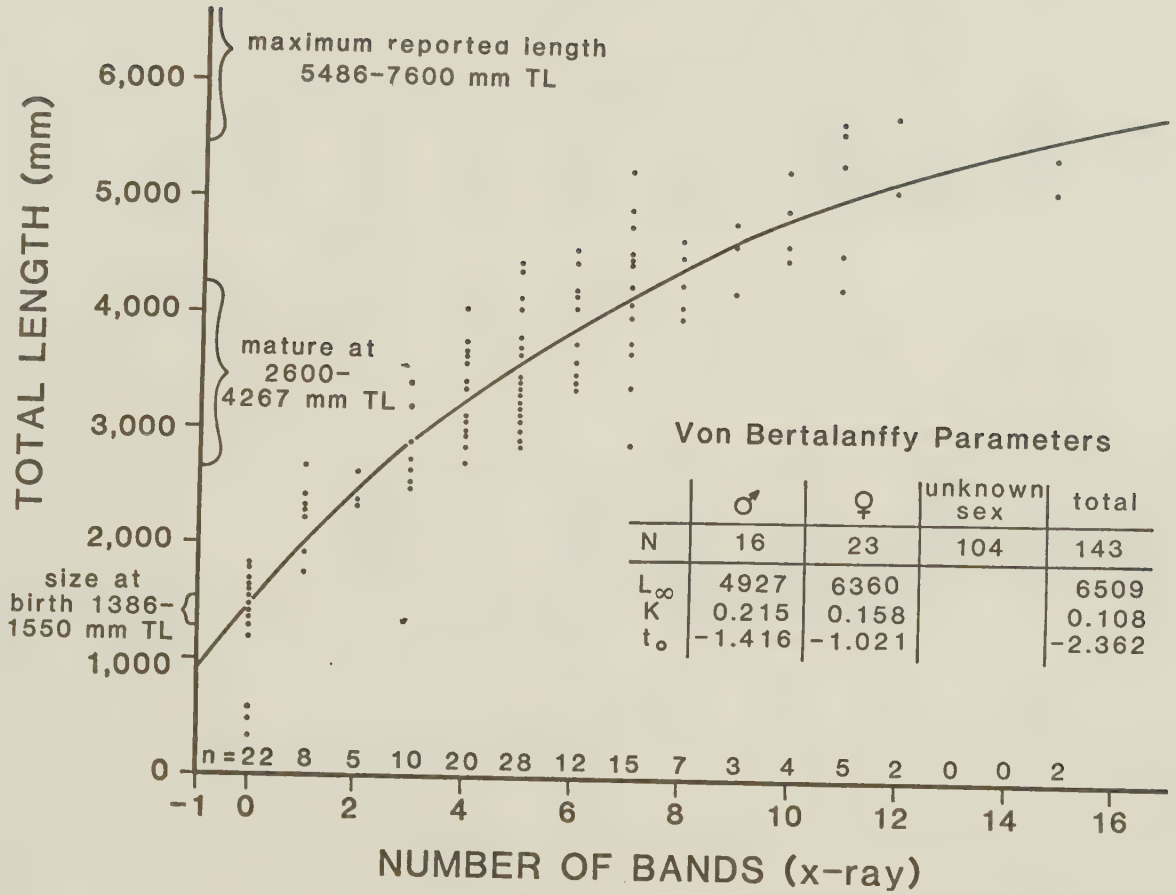

FIGURE 1. Von Bertalanffy growth curve for the common thresher shark from California waters based on x-radiography of vertebral bands (from Cailliet and Bedford, in press).

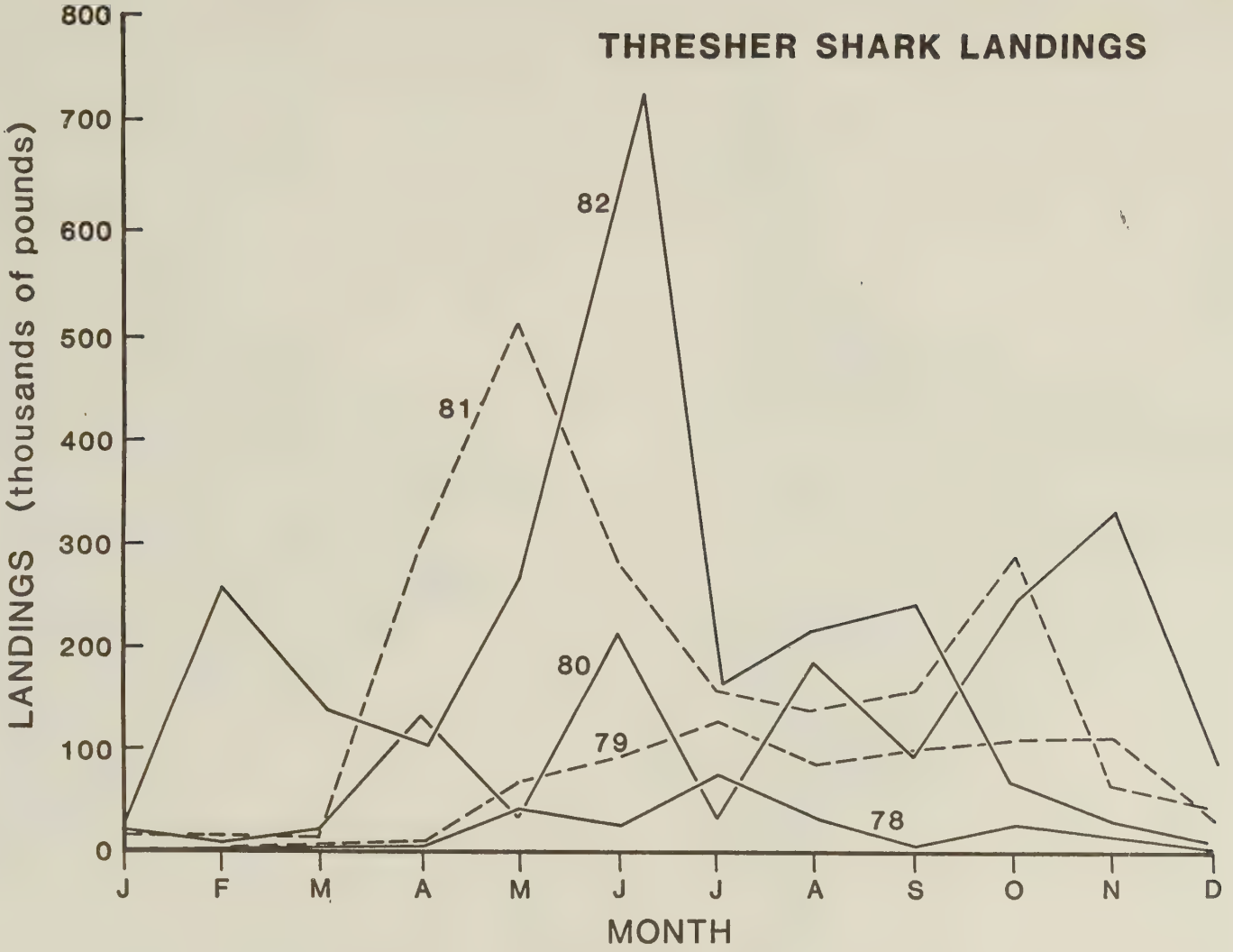

FIGURE 2. Monthly total thresher shark catches as reported from landing receipts.

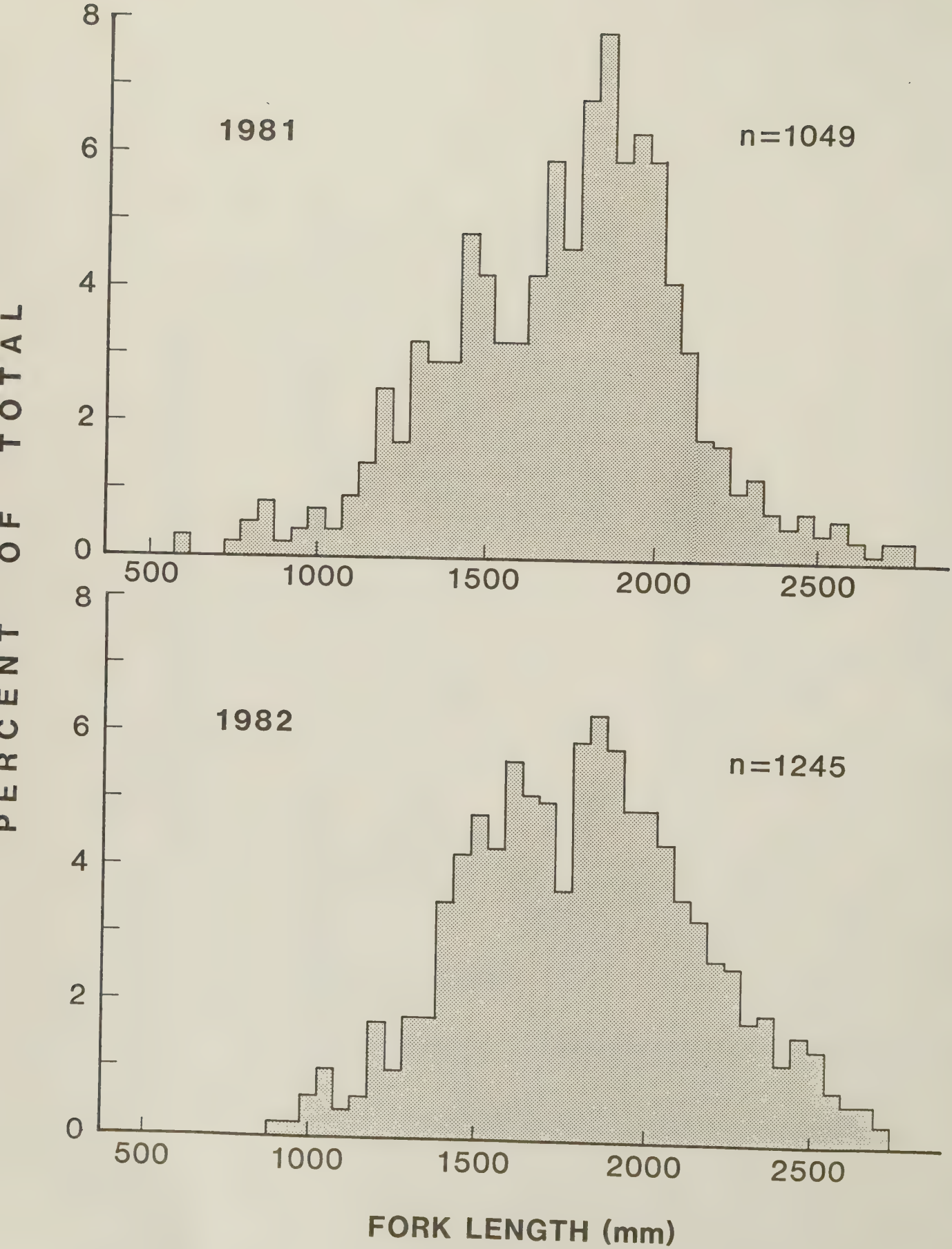

FIGURE 3. Common thresher shark length frequencies from samples taken as the shark were off-loaded from the fishing vessels.

APPENDIX A

Predicting Sustainable Harvest Rates From a Simplified Life Table of an Exploited Population

by

DOYLE ALAN HANAN

California Department of Fish and Game
c/o Southwest Fisheries Center
La Jolla, California 92038

and

ALEC D. MacCALL

National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

Predicting Sustainable Harvest Rates from a Simplified Life Table of an Exploited Population.

DOYLE ALAN HANAN AND ALEC D. MacCALL

ABSTRACT

Life table parameters necessary for equilibrium with a harvest are expressed in a simplified form of Lotka's equation, wherein harvest mortality rates are explicitly included. The main compensatory changes in the life table are decrease in age of maturity, and increased *per capita* recruitment, expressed as a product of fecundity and survival to maturity. The method reduces the number of parameters to a minimum, and allows demographic information to be incorporated in a variety of ways. Estimated harvest rates should be useful for development of poorly-known resources, and may be modified as information accumulates. Example applications are given for an arctic marine mammal (the ringed seal, *Phoca hispida*), a pelagic schooling fish (the Pacific sardine, *Sardinops sagax*), and a pelagic shark (the common thresher shark, *Alopias vulpinus*).

INTRODUCTION

The immediate effect of harvest is to reduce the abundance or density of a population. This reduction can be offset by compensatory changes in life table parameters, as has been identified for fish (Goodyear 1980), insects (Stubbs 1977), and mammals (Fowler 1980). In large, long-lived animals, these density-dependent responses may be difficult to identify since, as Fowler (1981) shows, the responses probably occur at high population levels (near carrying capacity). One such response is a decrease in the age of reproductive maturity which increases net cohort productivity and helps balance removals by harvest. Other density-dependent responses such as increased fecundity or higher survival rates may also occur in harvested populations.

To predict sustainable harvest with a minimum of information, we present models which predict the equilibrium harvest mortality given the adult survival rate and a change in the age of reproductive maturity and/or fecundity. The models are applied to a well-studied population of ringed seals (Phoca hispida) in the Canadian eastern arctic and to the sardine (Sardinops sagax) fishery of California. To demonstrate predictive uses, the models are also applied to thresher sharks (Alopias vulpinus), a resource about which little is known, but which has generated much interest due to an expanding fishery in the eastern North Pacific Ocean.

THE MODEL

Following Leslie (1966) and Mertz (1971), we divide the life table into juvenile and adult life stages i.e., reproductively immature and reproductively mature. In this model, stochastic variability in life table parameters is ignored and only females are modeled. Juvenile survival (β) is measured from the first birthday to the age of reproductive maturity (α). While individuals may vary in age of reproductive maturity, parameter α is interpreted as the mean age of reproductive maturity for the population. Adult annual survival (P) and annual fecundity (m) are assumed to be constant after reproductive maturity. Fecundity (m) also includes survival to the first birthday.

Combining these terms with the finite rate of population increase (λ) and assuming a stable age distribution, the collapsed geometric progression of abundance-at-age gives the following simple form of Lotka's equation:

$$\lambda^{\alpha} - p^{\alpha-1} - \beta m = 0 \qquad (1)$$

If we assume the population to be at equilibrium, the dominant root of the equation must be unity ($\lambda=1$) and the equation simplifies to

$$1 - P - \beta m = 0 \qquad (2)$$

which simply states that at equilibrium, adult deaths (1-P) are offset by recruitment (βm).

We assume an equilibrium rate of exploitation, in which harvest losses are compensated by a decrease of γ years in the age of reproductive maturity and/or an increase in fecundity. Harvest mortality rates are assigned to each life stage, by modifying P, β, and m in equation (1) to give

$$\lambda^{\alpha-\gamma} - p'\lambda^{\alpha-1-\gamma} - \beta' m' = 0$$

where P', β', and m' represent parameter values with a harvest.

Annual adult survival is multiplied by the probability of being harvested ($P' = Pe^{-f}$), where f is the instantaneous coefficient of harvest mortality, assuming unit time. In the absence of harvest, juvenile survival to maturity (β) is equal to the product of the age specific survival rates

$$\beta = \exp\left(-\sum_{i=1}^{\alpha-1} n_i\right) \qquad (3)$$

where n represents the age specific coefficient of natural mortality. With exploitation, the survival of juveniles would decrease due to harvesting mortality, and if the age of maturity also decreases, juvenile survival is further modified. For a decrease of γ years in the age of maturity, juvenile survival under exploitation (β') is given by

$$\beta' = \exp-\left(\sum_{i=1}^{\alpha-\gamma-1} n_i + f\phi_i\right) \qquad (4)$$

where f is the harvesting rate of adults and ϕ_i is age specific availability of juveniles relative to full adult availability. For example, if $\phi_i = 0.5$,

the harvest rate of the i^{th} juvenile age class would be one-half the harvest rate of adults. Equation (3) can be expanded to

$$\beta = \exp\left(-\left(\sum_{i=1}^{\alpha-\gamma-1} n_i + \sum_{i=\alpha-\gamma}^{\alpha-1} n_i\right)\right) \qquad (5)$$

which is algebraically rearranged to give

$$\exp\left(-\sum_{i=1}^{\alpha-\gamma-1} n_i\right) = \beta \exp\left(\sum_{i=\alpha-\gamma}^{\alpha-1} n_i\right) \qquad (6)$$

Substitution of equation (6) into equation (4), with $\Phi = \sum_{i=1}^{\alpha-\gamma-1} \phi_i$ gives

$$\beta' = \beta \exp(-\Phi f) \exp\left(\sum_{i=\alpha-\gamma}^{\alpha-1} n_i\right) \qquad (7)$$

The last term in equation (7) represents the juvenile mortality which no longer occurs between ages $\alpha-\gamma$ and α, due to the compensatory decrease in the age of maturity and the shortened juvenile period. Since the mortality rates immediately preceding maturity are likely to be similar to adult mortality rates, we make the simplifying assumption that adult survival rates apply. This allows further simplification to

$$\beta' = \beta \exp(-\Phi f) p^{-\gamma} \qquad (8)$$

Since harvest of juveniles may occur in the first year of life and the Leslie model does not census these animals until they complete the first year of life, a harvest mortality may be included in the fecundity term. Because β and m occur as a product, this mortality in age Ø individuals can be included by decreasing the lower limit from one to zero in the summation $\left(\Phi = \sum_{i=0}^{\alpha-\gamma} \phi_i\right)$ described above.

These modified terms are substituted into equation (2) to obtain:

$$1-Pe^{-f-\beta mP^{-\gamma}e^{-\Phi f}} = 0 \qquad (9)$$

which we call the general model and which can be solved iteratively for f, the equilibrium or sustainable harvest rate. This model describes a surface of sustainable f values when plotted with respect to P and βm as shown in figure 2. From equation (2) we see that at unharvested equilibrium, adult mortality (1-P) must be offset by recruitment, the product of juvenile survival and fecundity (βm). If we make the assumption that there are no density-dependent changes in juvenile survival or fecundity, we can further simplify the model by substituting 1-P for βm in equation (9) to obtain:

$$1-Pe^{-f-(1-P)P^{-\gamma}e^{-\Phi f}} = 0 \qquad (10)$$

This more conservative model, termed the restricted model, allows only for a change in the age of reproductive maturity as the compensatory response to harvest. Notably, the restricted model has reduced the number of necessary parameters to a minimum, requiring estimates only of adult survival rate, change in age of maturity, and the number of harvested juvenile age classes. If these parameters are unknown, they can be estimated, depending on the degree of information available for the species in question. For example, to apply the model to thresher sharks, we estimated adult survival (P=0.93) based on growth information from Cailliet and Bedford (1983) and a comparative method for estimating natural mortality rates (Pauly 1980).

Although the models are based on a discrete-time Leslie matrix, the collapsed forms of both equations (9) and (10) allow parameter λ to take on non-integer values with interpretable results. This is useful, since population parameters such as mean or median age of maturity commonly act as continuous variables.

In some cases fecundity has been estimated for both exploited and unexploited populations (Perrin, Coe and Zweifel, 1976; Perrin, Holts and Miller, 1977). For those conditions, equation (2) allows β to be defined in terms of unexploited fecundity (m_o)

$$\beta = (1-p)/m_o \qquad (11)$$

This value of β can be substituted into the general model equation (9) to provide a "change in fecundity model"

$$1-pe^{-f}-(m_e/m_o)e^{-\Phi f}(1-p)p^{-\gamma} = 0 \qquad (12)$$

where m_e is the fecundity of the exploited population. This form allows the ratio m_e/m_o to be substituted for the difficult-to-estimate parameters β and m.

RELATIONSHIP TO "POTENTIAL YIELD"

Alverson and Pereyra (1969) proposed a rule-of-thumb for fishery development wherein sustainable fishing mortality rate is assumed to be equal to the

natural mortality rate. Gulland (1970) expanded this idea and applied it to a variety of poorly studied, underutilized fish stocks. The Alverson-Pereyra-Gulland (APG) potential yield formula was originally intended as an initial guess of fishery potential, to be applied in a spirit similar to the method we have proposed. The usual form of the APG formula includes a further assumption of a logistic production model; that aspect of the formula is not amenable to examination by our life table model.

The APG formula lacks a theoretical basis, and its utility has not yet received adequate empirical substantiation. Francis (1974) examined the theoretical relationship between the APG formula and stock-recruitment relationships, and demonstrated some conditions necessary for the formula to be valid. Here we similarly use our model to examine the theoretical implications of the APG formula in terms of basic life-history parameters.

The general model (equation 9) can be rearranged to express per capita recruitment (βm) as a function of the other parameters:

$$m = (1-Pe^{-f})p^{\gamma}e^{\Phi f} \qquad (13)$$

This can also be expressed in terms of the instantaneous rate of adult mortality ($N = -\ln P$), giving

$$m = (1-e^{-(f+N)})e^{\Phi f-\gamma N} \qquad (14)$$

The APG formula assumes that f = N is sustainable, requiring the relationship

$$\beta m = (1-e^{-2N})e^{-N(\gamma-\Phi)} \qquad (15)$$

or, in terms of annual survival,

$$\beta m = (1-p^2)p^{\gamma-\Phi} \qquad (16)$$

Equation (16) describes a line on the surface of sustainable f values shown in Figure 1. This line is the intersection of the surface described by equation (13) and another surface described by the APG potential yield assumption of f = -ln P.

Alternatively, we can express equation (16) in terms of the relative increase (δ) in per capita recruitment, where δ is defined by the relationship

$$(\beta m)_e = (1+\delta)\ (\beta m)_o \qquad (17)$$

and the subscripts represent exploited (e) and unexploited (o) values respectively. The unexploited per capita recruitment is given by equation (2), so the APG formula requires that

$$\delta = (1+p)p^{\gamma-\Phi}-1 \qquad (18)$$

Thus, equations (16) and (18) provide objective criteria for judging the performance of the APG potential yield formula. The necessary parameters can

be obtained by standard fishery monitoring and analysis as exploitation of the resource progresses.

APPLICATION OF THE MODELS

To validate the utility of the models, fairly detailed life table data, population estimates, and catch statistics are needed. Smith (1973) provides an excellent summary of such data on ringed seals at Baffin Island, Canada. The age of reproductive maturity in these seals appears to have declined, probably in response to harvest. Smith also states that the population is in equilibrium.

Smith's data are based on a 5-year sampling program (1966-1970) and on information from earlier studies, especially McLaren (1958a,b). The study area (Figure 2) was the east coast of Baffin Island, including lightly harvested populations in Home and Hoare Bays, and a heavily harvested population in Cumberland Sound. Smith shows that production of seals in the fast ice areas near the Sound contributes seals to the Sound; therefore, we consider seals in the Sound and the immediately adjacent areas, Cape Dyer to North Foreland (i.e. McLaren's (1958b) areas 5, 6, and 7), to be a single stock for purposes of analysis.

Smith's (1973) population estimates compare well to those of McLaren (1958a,b), supporting the assumption that the population is in equilibrium. The Heinke (1913) survival rate estimator gives adult (0.88), juvenile (0.85), pup (0.59), and whole population (0.72) annual survival rates from Smith's

catch curves. Baranov's catch equation (Ricker 1975, equation 1.17) was used to remove harvest mortality from these rates, giving adult (0.94), juvenile (0.91), and pup (0.69) estimates of annual natural survival.

Smith (1973) and McLaren (1958a) demonstrate from ovarian criteria that female ringed seals from most areas mature sexually at 7+ years, while those from the heavily exploited Home and Hoare Bays mature at 4+ to 5+ years, indicating a 2- or 3-year decline in age of maturity due to harvesting. Smith also estimates a mean yearly reproductive rate of 0.8 per female and a 1:1 sex ratio of the pups. Combining this with the pup survival rate gives a female *per capita* production of 0.28 daughters surviving to the first birthday.

The population estimate from McLaren (1958b) for the Cumberland Sound stock (areas 5, 6, and 7) was 134,800 seals. According to the stable age distribution of Smith (1973), the number of seals in each age group would have been approximately: adults 68,411; juveniles 40,898; and pups 25,491. While the catch curves from Smith (1973) show the mean annual catch (9262) by age to be: adults 4,087; juveniles 1,982; and pups 3,193. These estimates, along with the survival rate estimates, were used in the catch equation to estimate the actual harvest mortality for comparison to values predicted in our model.

Given the ringed seal survival and fecundity estimates, less harvest mortality from the catch equation, we applied both the general and the restricted models. The general model predicts a sustainable harvest mortality of 0.069 for a 1-year decline in age of maturity, 0.089 for 2-year decline, and 0.113 for a 3-year decline. The restricted model predicts 0.003 for a 1-

year decline, 0.006 for a 2-year decline, and 0.01 for 3-year decline. Baranov's catch equation, based on a population of 134,800 seals, a harvest of 9,262 seals, and the whole population survival estimate of 0.72, estimates 0.081 as the actual yearly harvest mortality in the Cumberland Sound stock for the period of Smith's study. This result is in good agreement with the prediction of the general model, considering the many potential violations of simplifying assumptions.

Smith (1973) shows that only about 40% of the Home and Hoare Bay females are reproductive at age 4+ and those that are probably do not become pregnant until the year after maturity. This means that γ actually equals one or two, and the predicted harvest mortality range (0.069 to 0.089) narrows to bracket the actual harvest mortality even more closely.

The relationship of the general and restricted models is demonstrated in Figure 1, where P, m, and predicted equilibrium f are plotted for a fixed value of γ. The general model produces a surface of possible f values and the restricted model produces a line of predicted f that extends diagonally across that surface. Predicted f values below that line are not plausible since βm is unlikely to decrease in response to exploitation. Predicted f values above that line represent the area where βm has increased over its pristine value (1-P), as shown in the ringed seal data, thus allowing a greater sustainable harvest than is predicted by the restricted model. The difference between harvest mortality predicted by the general model and the restricted model also reveals the comparative strengths of the two density-dependent responses. Decreased age of reproductive maturity appears to be a much weaker response

than increased recruitment rate (βm), as is further exemplified by plotting the f values generated (Fig. 3) for γ equals one to three and the effect of a 50% increase in βm. These graphs reveal that even small increases in recruitment are much more compensatory than changes in age of reproductive maturity for long-lived species.

APPLICATION TO A SHORT-LIVED SPECIES

Both the California sardine (Sardinops sagax) and the South African sardine (Sardinops ocellata) showed decreases in the age of reproductive maturity in response to fishery-induced population declines (Crawford, Shelton, and Hutchings 1980; Murphy 1966, 1977). Without delving into the stock-recruitment aspects of these fishes' population dynamics, our simplified life table approach can answer the question: "Approximately how much of the sustainable harvest rate is due to earlier reproductive maturity ?".

Life table parameters of the California sardine have been estimated by Murphy (1966, 1977) and MacCall (1979). Annual mortality of adults is 0.67, and 2-year old fish are half as vulnerable to fishing as 3-year and older fish. During the early years of the fishery, one-half the 2-year olds and all older fish were reproductively mature. Later, all 2-year old fish were reproductively mature (Murphy 1966), a shift of approximately one-half a year in average age of maturity. The restricted model (i.e. ignoring other compensatory changes in life table parameters) indicated that this decrease in age at maturity would be balanced by a harvest rate of $f = 0.087$. Murphy (1967) estimated the intrinsic rate of increase of California sardines to be

0.34, and this should be close to the maximum sustainable harvest rate. MacCall (1979) estimated from simulations based on observed reproductive rates that f = 0.25 was about the maximum rate that the sardine could have sustained. Thus, the harvest rate supported by the change in age of maturity is a sizeable fraction (one-quarter to one-third) of the overall sustainable rate of harvest for California sardines. In general, the simplified life table model indicates that short-lived (low annual survival) species will tend to benefit more than long-lived species from decreases in age of maturity.

APPLICATION TO A NEW FISHERY

To demonstrate a possible use of our method as a management tool, it is applied to the thresher shark. Since this shark has not been extensively studied, biological and life table data are scarce; therefore, in applying the model we use the range of values most likely to bracket the expected life table parameters. These parameters are apparently similar to many mammals in that the thresher shark has low fecundity (two to four pups per year), matures at an older age (7 to 9 years; Cailliet and Bedford 1983), and appears to have a high adult survival rate (above 0.85 annually).

The thresher shark is ovoviviparous and the embryos may limit competition *in uteri* by eating additionally produced eggs (Holden 1973). At birth they are large (1.0 to 1.5 meters), well-developed, and probably have a high juvenile survival rate. For these reasons, we assume that the primary density-dependent response offsetting the harvest would be a decrease in the age of reproductive maturity. Thus our restricted model should be applicable to initial management of this resource.

Sustainable fishing mortality rates ranging from 0.007 to 0.049 are predicted by the restricted model for adult survival rates of 0.9 to 0.85 and 1 to 3 year declines in the age of reproductive maturity. While these seem to be very low harvest mortality rates, historical experience of shark fisheries has shown shark resources to deplete quickly when harvested (Ripley 1946; Holden 1974).

CONCLUSION

The predicted harvest levels from the restricted model are conservative since the model only allows for density-dependent changes in the age of reproductive maturity. However, these predicted harvest rates provide useful initial estimates for rational resource management and may be modified as historical harvest and biological data accumulate. Initial parameter estimates may be based on comparative information from better-known resources. For example, using only the ringed seal estimates of adult survival and age of reproductive maturity, we would have predicted a sustainable harvest mortality ranging from 0.003 to 0.01 depending on likely values of γ (1 to 3 years). These harvest mortality predictions are well below that subsequently shown to be sustainable and, in the absence of additional biological information, these estimates would have been a safe first guess for management purposes.

We use the restricted model to obtain initial estimates of sustainable harvest rates for the thresher shark. Those values are probably close to the maximum sustainable values, if our assumption holds that a change in is the dominant compensatory response in these animals.

Finally, we have presented a method which requires minimal biological information to predict sustainable harvest mortalities, and we feel that the method is quite adaptable to many little-studied resources for management purposes. While the approach is designed for long-lived species, the logic also has potential application to relatively short-lived species such as fishes, birds, and small mammals.

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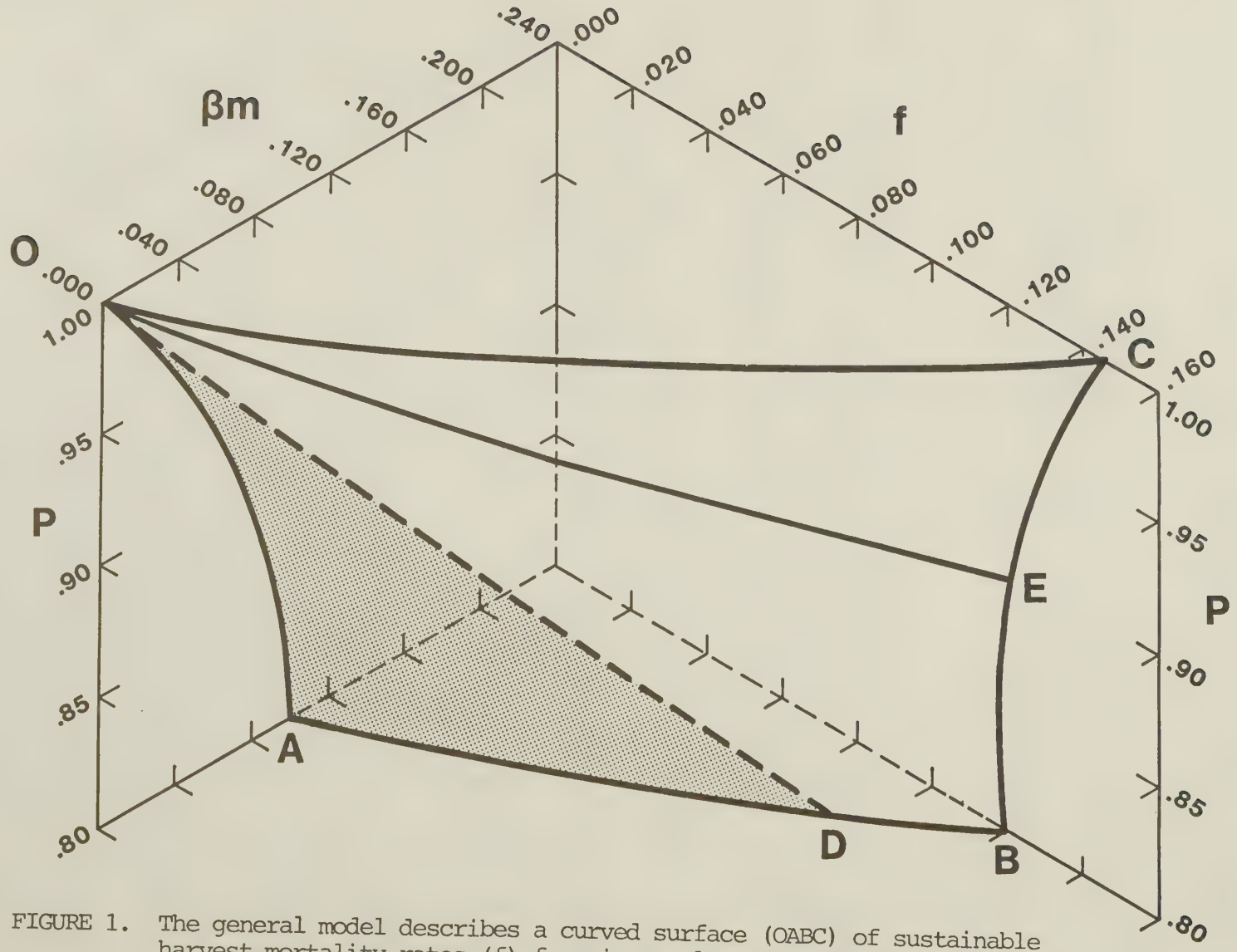

FIGURE 1. The general model describes a curved surface (OABC) of sustainable harvest mortality rates (f) for given values of adult survival (P) and per capita recruitment (Bm). The restricted model predicts f as a line (OD) across that surface. The shaded area below OD represents rates of f not likely to occur as they would require Bm to decrease in response to harvest. Predicted f from the APG potential yield model is shown as line OE on surface OABC; $\alpha = 3$, $\Phi = 4$.

FIGURE 2. East coast of Baffin Island in the Canadian eastern Arctic.

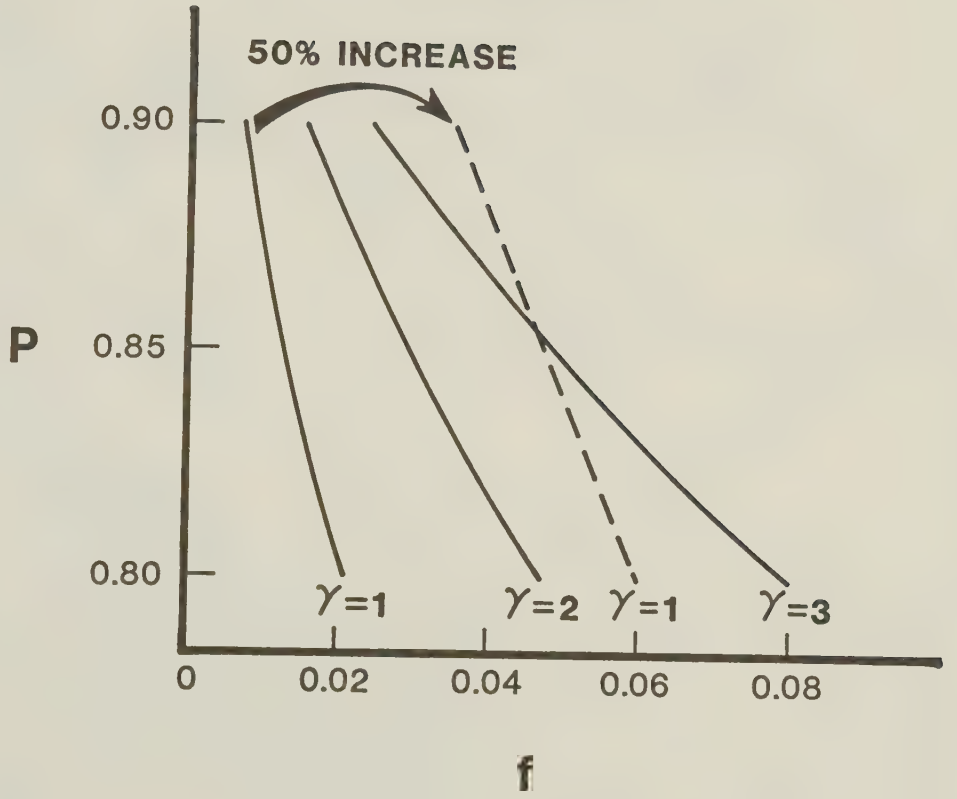

FIGURE 3. Predicted sustainable harvest mortality rates (f) are represented for given adult survival rates (p) and declines of one, two, and three years in the age of maturity (γ) as predicted by the general model. Also shown is the effect on f of a 50% increase in Bm for γ=1 to be compared to the two and three year changes in γ.